



Perch selection in a guild of tropical dragonflies (Odonata: Libellulidae): relationships with body size and thermal ecology

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In the temperate zone, male perch height of co-occurring dragonfly species (Odonata: Libellulidae) often correlates with species body size. I tested for this relationship in a guild of tropical dragonflies at a wetland at La Selva Biological Station, Heredia, Costa Rica. Males of 12 species were observed perching in January–February 2016. Mean male perch height was positively correlated with species body size. For six common species, I quantified differences in perch substrate selection, relationships between diurnal activity, temperature and radiation, and aggressive interactions. The largest species, *Libellula herculea* and *Orthemis discolor*, exhibited typical heliotherm behavior: they used sunny perches at mid-day, and activity correlated more with radiation than temperature. *Orthemis cultriformis*, a slightly smaller heliotherm, was active at mid-day but used shadier perches. *Micrathyria atra* – previously classified as a “behavioral endotherm” – behaved accordingly, avoiding over-heating by flying early and perching in moderate light. The smallest common species, *Erythrodiplox fervida*, departed from the expected “thermo-conformer” behavior by showing no relationship between activity and temperature, perching throughout the day in shaded grasses. The medium-sized *Cannaphila insularis* was unusual, perching 1 m higher than other species. Like larger heliotherms, activity occurred mid-day and correlated with solar radiation. Larger species exhibited greater degrees of interspecific aggression than smaller species. *Cannaphila insularis* is a docile species, but juveniles and females resemble the larger, more aggressive *O. cultriformis*. I hypothesize that *C. insularis* perches high to escape harassment and “reproductive interference” by *O. cultriformis*.

Keywords: dragonfly; community ecology; niche partitioning; perch selection

Introduction

Perch selection by territorial male dragonflies has important consequences. It can affect access to mates and food (Baird & May, 1997; Martens, 2001; May, 1984; Van Buskirk, 1986), susceptibility to predators, susceptibility to intra- and interspecific aggression (De Marco & Resende, 2004; Eason & Switzer, 2004; McCauley, 2010; Rehfeldt & Hadrys, 1988; Switzer & Walters, 1999), and thermoregulation (De Marco, Latini, & Resende, 2005; May, 1976, 1978, 1991). In most communities of perching dragonflies, species exhibit different perch preferences, perching on different substrates, in different microhabitats, at different heights, and at different times of the day (De Marco, 1998; Guebailia et al., 2016; Khelifa et al., 2013; Lutz & Pittman, 1970; Osborn & Samways, 1996; Parr, 1983; Raab, Chovanec, & Wiener, 1996; Reinhardt, 1999; Resende & De Marco, 2008). Not surprisingly, these temporal and spatial patterns of habitat use often correlate with body size (Peters, 1983; Rasmussen, Van Allen, & Rudolph, 2014).

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Body size affects the thermoregulation strategy of dragonflies (Corbet, 1962; Corbet & May, 2008), and so affects temporal and spatial patterns of perch selection. For example, in contrast to “fliers” that are large enough to generate heat endothermically and tend to patrol continuously during periods of activity (Corbet & May, 2008; Heinrich & Casey, 1978), “perchers” tend to be either small thermoconformers (dependent on appropriate air temperature for flight) or larger “heliotherms” that can achieve flight temperature by basking (De Marco & Resende, 2002; May, 1976, 1991). In warm environments, small thermoconformers will be most active in the cooler morning and afternoon hours and will use shaded perches or postural changes like “obelisking” to avoid overheating (Corbet & May, 2008). Heliotherms will use sunny perches and will be active for short periods during the sunniest hours of the day. Small thermoconformers seeking shade may perch in low weeds or grasses, but larger heliotherms – that grass blades cannot support – will perch on taller, sturdier, sunlit perches like twigs, vines, or tree-trunks, or on sunlit patches of ground. So, several aspects of perch selection can be direct consequences of body size and thermal niche.

Size-related differences in perch and habitat selection may also be a product of interspecific interactions, typically with larger species excluding smaller species from preferred habitats (Khe-lifa, et al., 2013; Moore, 1964; Pezalla, 1979; Rehfeldt & Hadrys, 1988). In the temperate zone, perch height of territorial male libellulids often correlates with species’ body size (Moore, 1991; Warren, 1964; Worthen & Jones, 2006). This is often a consequence of a size-dependent competitive hierarchy where large species tend to displace smaller species from tall perches (Worthen & Jones, 2006; Worthen & Morrow, 2016; Worthen & Patrick, 2004). This can even create the non-random pattern of “species packing”, with a regular increase in mean perch height corresponding to a regular increase in mean body size (Worthen & Jones, 2007). These patterns are probably the result of both adaptive responses to persistent competitive interactions (which constrain a suitable range of perch heights for each species and generate “species packing” patterns in mean perch heights), and behavioral shifts in perch height in response to proximate competitors. For example, *Perithemis tenera* Say typically perch at heights of 3–30 cm (probably an adaptive constraint), but perch lower in this range when larger competitors are nearby (Worthen & Patrick, 2004).

However, this size-dependent competitive hierarchy does not hold in all communities. In Singer’s (1989) study of interspecific aggression among three *Leucorrhinia* species, the smallest species was both more aggressive and more successful in interspecific encounters (maintained their territory) than the largest species. Likewise, in Resende’s (2010) study of five similar *Erythrodiplax* species, territorial residency determined the winner of heterospecific contests more than the mean body size of interacting species. Of course, size-dependent hierarchies will be more likely where size differences are more dramatic. When species are similar in size, these patterns will probably be more variable (Worthen & Morrow, 2016). In these cases, factors that determine success in intraspecific contests – such as differences in individual body size, fat reserves, age, flight muscle mass, immunocompetence, parasite load, or residency (reviewed in Suhonen, Rantala, & Honkavaara, 2008) – are probably more important than mean differences in species’ body sizes.

The purpose of this investigation was to describe patterns and causes of perch-height selection in a guild of tropical perching dragonflies. Few studies in the tropics have explicitly addressed this question at the community level. Rather, most have appropriately measured perch height as one of several niche parameters, including substrate, microhabitat, distance from shore, and diurnal activity patterns, usually in the context of testing the relevance of different thermoregulatory strategies among subsets of resident species (De Marco, 1998; De Marco et al., 2005; De Marco & Resende, 2002, 2004; Resende & De Marco, 2008). Specifically, I tested the hypothesis that male perch height correlated with mean species body size, and results from a size-dependent competitive hierarchy. I also described differences in perch substrate preference and temporal

patterns of activity, and related these patterns to the “thermoconformer – heliotherm” dichotomy of “percher” thermoregulation.

Methods and materials

Site description

This survey was conducted from 20 January to 9 February 2016, in the Cantarrana wetland at the La Selva Biological Station of the Organization for Tropical Studies (OTS) in Heredia Province, Costa Rica (10.42923 N, – 84.005697 W). The wetland is approximately 100 m × 30 m, within old-growth lowland tropical rainforest. La Selva receives approximately 4 m of rainfall annually; monthly rainfall typically exceeds 400 mm in June, July, and August, declining to less than 120 mm per month for February and March (Sanford, Paaby, Luvall & Phillips, 1994). During the rainy season, water fills the wetland from forested bank to forested bank, covering all but the tallest aquatic macrophytes. During this survey, however, at the onset of the dry season, open water was relegated to 3–4 widely separated shallow muddy pools that shrank over the sampling period. Approximately 80% of the wetland was covered by marsh grasses and sedges, and a few isolated saplings grew from hummocks or nurse logs. Several wind-thrown tree limbs, and trees on the periphery of the wetland, also provided perch sites for dragonflies.

Sampling procedure

I observed dragonflies each day, during rainless periods from 08:00–16:00 h, from an elevated boardwalk that bisects the wetland. I walked the length of the boardwalk every 30 min, recording as many perch events as possible. A perch event was recorded when a dragonfly was observed to alight on a perch. Repeated perch events by the same individual, even on the same perch, were recorded as separate and independent perch events. Individuals could not be captured and marked, and so individuals were resampled throughout each sampling day and across the sampling period. The degree to which I was measuring individual behavior or the generalized behavior of the species was confounded, especially for species represented by a few individuals that perched often. Estimated abundances and the number of perch events recorded are presented for comparison (Supplemental Table S1).

For each perch event, I recorded the species and sex of the dragonfly, substrate (grass, tree, downed branch), light conditions at the perch (sunny, moderate, shady), and height of the perch above the walkway. Average hourly temperature (°C) and average hourly solar radiation (W m^{-2}) were computed using meteorological data reported every 30 min, from datalogger readings taken every 10 s, at a weather station approximately 500 m from the study site (Organization for Tropical Studies, 2016). I measured perch heights by shooting a leveled laser beam at perches from one of seven sighting stations along the boardwalk (Figure 1). A Checkpoint Inclo-Matic Laser Level (#0675)[®] (Checkpoint Levels, Inc., Pacoima, CA, USA) and Laserscope[®] (Shenzhen Vokul Sports Equipment Corp., Shenzhen, Guangdong, China) were mounted on a carriage of 1.905 cm (0.75 in) PVC pipe and joints, that slid up and down along a 2.2 m measuring staff (Bioquip[®] insect net handle (7312AB) with affixed measuring tape) (Bioquip Products, Inc., Rancho Dominguez, CA, USA) (Figure 1a). The height above the boardwalk (at that sighting station) was recorded when the level laser beam hit the perch, while holding the measuring staff as erect as possible (Figure 1b). This method allowed me to measure perch heights from a distance, without disturbing the dragonfly.

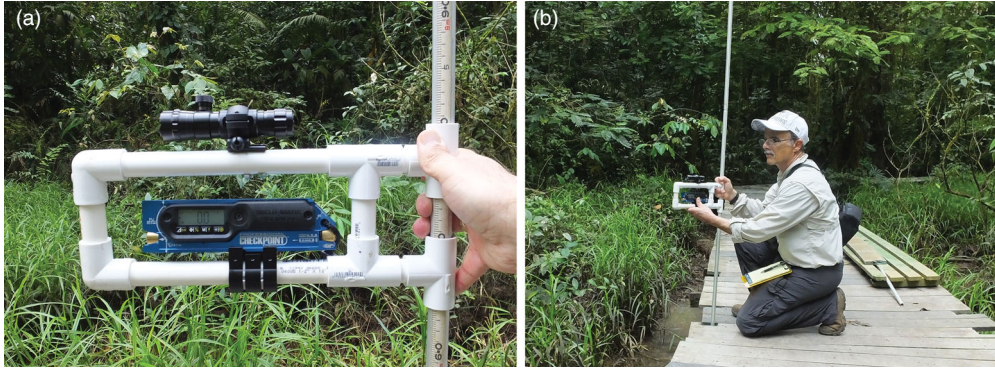


Figure 1. (a) Level and laserscope apparatus for measuring perch heights of dragonflies (the PVC “carriage” slides along the measuring shaft); and (b) sighting technique.

Collecting is not permitted in the wetland, so perching dragonflies were tentatively identified in the field using Pentax® 62001 6.5 × 21 mm Papilio II binoculars (Ricoh Imaging America Corp., Denver, CO, USA) and photographed with a Fujifilm® hs50exr camera (42 × optical zoom magnification) (Fujifilm North America Corporation, Wayne, NJ, USA) for later identification using available field guides (Esquivel, 2006; Haber & Wagner, 2011; Paulson, 2014, 2015). Voucher photographs of each species and sex were graciously examined by Dennis R. Paulson, who confirmed my identifications. Body lengths for each species (limited to males, if possible) (Shenzhen Vokul Sports Equipment Corp., Shenzhen, Guangdong, China) were computed by averaging the following values: the midpoint of size ranges reported by Haber and Wagner (2011), the midpoint of size ranges reported by Esquivel (2006), and the length of specimens reported by Paulson (2014). All species were represented in at least two of these sources (Supplemental Table S1).

I also recorded interactions between dragonflies, defining a “chase” if one dragonfly pursued another (either from a perch or in flight) and an “attack” if a dragonfly engaged a perched dragonfly. These categories were pooled as “aggressive behaviors”, identifying the species that was the aggressor and the target.

Data correction and standardization

It was difficult to steady the laser apparatus in perfectly accurate three-dimensional conformation by hand, but introduced error can be reasonably approximated. “Yaw” was eliminated by precisely sighting the beam on the target. “Pitch” was controlled by levelling the apparatus to 0.0°. With a level accuracy = $\pm 0.1^\circ$, and at a maximum distance of 15 m (from the boardwalk that roughly bisects the 30 m wide wetland), this equates to a maximum vertical error of 2.62 cm ($1500 \text{ cm} \times \sin(\theta)$). Most measurements were made at a distance of 5–10 m (to identify species), which equates to an error of 0.85–1.74 cm. The third axis, “roll”, was approximated by eye. While this represents unquantified human error, reasonable deviations impart only a small effect on vertical height estimates. For example, with the apparatus tilted at 10° from zenith, a 1.0 m perch height would be recorded as 1.015 m ($\sec(\theta)$); a deviation of only 1.5 cm. Even at 10° , however, the top of the 2.2 m measuring shaft would be deflected 38.8 cm ($220 \text{ cm} \times \tan(\theta)$) from the zenith – a departure that is easily recognized by eye. A more reasonable error of 10 cm off zenith at the top of the staff, corresponding to an angular error of 2.60° , would add an error of only 1.0 mm to the height of a 1.0 m perch ($\sec(2.60^\circ) = 1.00103$). Consequently, I am confident that heights up to 2.0 m, taken within 15 m, are within ± 2.0 cm of the true height above the sighting station.

Some individuals, particularly in the species *Cannaphila insularis*, perched higher than 2.2 m above the boardwalk – usually on the branch of a tree. Perches higher than 2.2 m above the boardwalk were estimated by shooting the laser to the trunk of the tree at 2.0 m and then extrapolating an estimated height to the nearest 0.10 m.

The boardwalk was uneven, so the sighting stations were not the same distance above the waterline. In addition, given the reduced and variable extent of water in the wetland, many sighting points were above dry land on any given day. Therefore, differences in the height of the sighting points above the waterline were corrected for by measuring the height of a common target from each sighting point, each day. The target was a support pole for the boardwalk that was above the central pool of the wetland. The height of this standard above the waterline in the central pool was measured each day, and a correction was applied to the height measurements made from each sighting point.

Statistical analyses

All analyses were limited to males. The mean perch height of males was compared between species using a one-way ANOVA and Tukey's multiple comparison test. I tested the hypothesis that perch height increases with body size with a one-tailed Pearson correlation.

The frequency of aggressive interactions between species were compared with chi-squared goodness-of-fit tests, comparing observed rates at which species attacked (and were attacked by) other species to expected frequencies based on the relative abundance of the species in the habitat over the entire sampling period. Relative abundances were estimated by the relative abundance of observed perch events.

A chi-squared test of independence was used to determine whether different substrates (trees, branches, or grass) were used to the same degree by all species. Chi-squared goodness-of-fit tests were used to describe preferences for a perch substrate by each species. Diurnal patterns of activity were described by comparing the frequency of perch events each hour, by each species. Raw frequencies were weighted prior to analyses, to correct for differences in sampling effort made for each hourly interval (range was 11–18) over the sampling period. A chi-squared test of independence was used to determine whether patterns of diurnal activity varied among species. Separate chi-squared goodness of fit tests were used to determine whether each species showed an uneven pattern of activity over the course of the day. For each species, the relationship between hourly activity values (response variable) and mean hourly temperature and mean hourly radiation (explanatory variables) was described in multiple linear regression analysis (climatological data from: Organization for Tropical Studies, 2016). All statistical analyses were conducted using SPSS®, version 21 (IBM Corp., 2012).

Results

There were significant differences in male mean perch height among the 12 species sampled (one-way ANOVA, $F = 85.733$, $df = 11, 1223$, $p < 0.0001$; Figure 2), and mean perch height was significantly positively correlated with mean body length (Pearson correlation, one tailed, $r = 0.530$, $p = 0.038$). *Uracis imbuta* (Burmeister) males had the lowest perch height, followed in ascending order by *Erythrodiplax umbrata* (L.), *Erythrodiplax fervida* (Erichson), *Anatya guttata* (Erichson), and *Erythrodiplax kimminsi* Borror, that all had mean perch heights within 1 m of the waterline (Figure 2). Males of *Micrathyria atra* (Martin), *Micrathyria laevigata* Calvert, *Orthemis cultriformis* Calvert, *Orthemis discolor* (Burmeister), *Orthemis schmidtii* Buchholz, and *Libellula herculea* Karsch perched at intermediate levels, with mean perch heights between 1.3

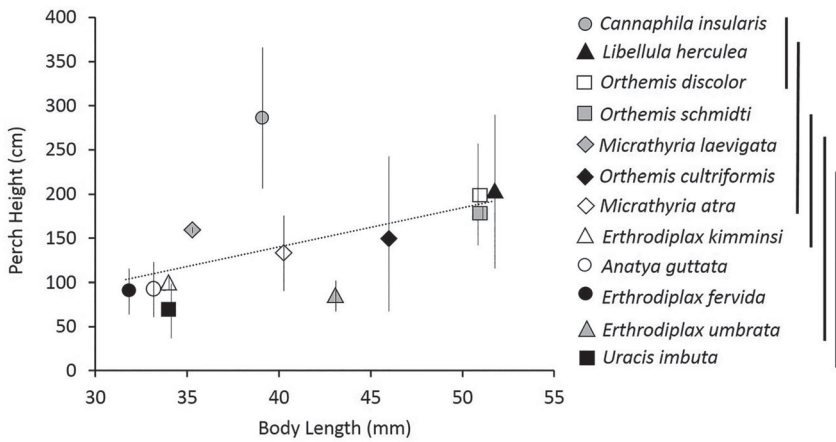


Figure 2. A comparison of mean (± 1 SD) male perch heights of 12 libellulid species in the Cantarrana Wetland, La Selva Biological Preserve, Heredia, Costa Rica, and the relationship with mean body size. (Species connected by the same line are not significantly different in mean perch height; Tukey mean comparison test, $p = 0.05$. Pearson correlation between mean perch height and mean body size: $r = 0.530$, $p = 0.038$, Pearson one-tailed test.)

and 2.0 m (Figure 2). *Cannaphila insularis* Kirby males perched highest, almost 1 m above the next highest species (Figure 2). The differences between significantly different groups exceeded the error of the apparatus (estimated at ± 2.0 cm). Although I assume that all species used the site for mating and oviposition, I only observed this for *M. atra*, *O. cultriformis*, *O. discolor*, *L. herculea*, and *C. insularis*.

Among the six most abundant species ($N > 30$ for male perch events), there were significant differences in species preferences for perch substrates ($\chi^2 = 663.09$, $df = 10$, $p < 0.0001$, Figure 3). Grass was strongly preferred by the smallest species, *Erythrodiplax fervida*

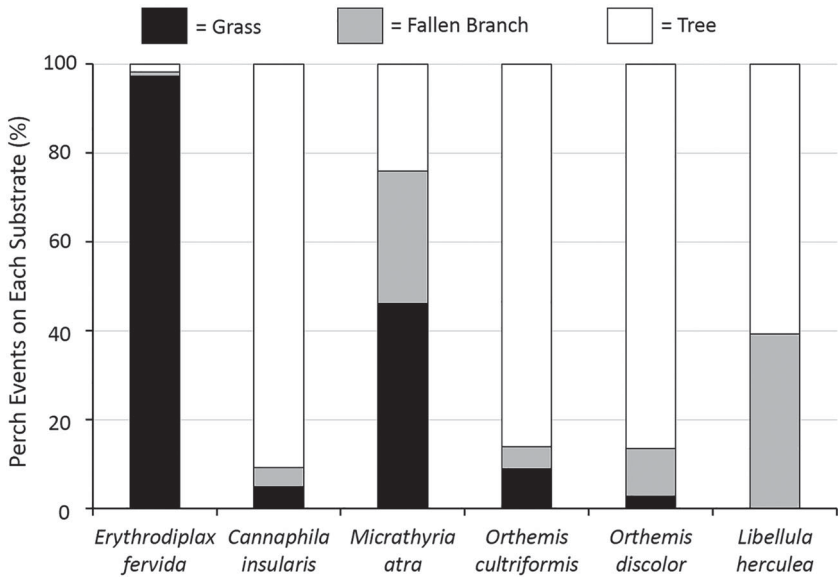


Figure 3. The proportion of grass, branch, and tree substrates used as perches by males of the six most abundant species of libellulids in the Cantarrana Wetland, La Selva Biological Station, Heredia, Costa Rica. Species are ordered by body size from small to large. Species differ in their substrate preferences (see results), and preference for grass is inversely correlated with mean body size (two-tailed Pearson correlation, $r = -0.8830$, $df = 4$, $p = 0.038$).

($\chi^2 = 208.37$, $df = 2$, $p < 0.0001$); *M. atra* also preferred grass ($\chi^2 = 33.06$, $df = 2$, $p < 0.0001$) but often used other substrates (Figure 3). Trees were preferred by *C. insularis* ($\chi^2 = 211.37$, $df = 2$, $p < 0.0001$) and the three largest species: *O. cultriformis* ($\chi^2 = 126.97$, $df = 2$, $p < 0.0001$), *O. discolor* ($\chi^2 = 142.22$, $df = 2$, $p < 0.0001$), and *L. herculea* ($\chi^2 = 108.70$, $df = 2$, $p < 0.0001$; Figure 3). Species body size was inversely correlated with the percentage of perches in grass (Pearson correlation, two-tailed, $r = -0.8830$, $df = 4$, $p = 0.039$).

These six species also varied in temporal activity patterns (χ^2 test of independence, $\chi^2 = 333.90$, $df = 35$, $p < 0.0001$, Figure 4). *Micrathyria atra* was significantly more active in the mornings than after noon ($\chi^2 = 70.99$, $df = 7$, $p < 0.0001$). Four species were significantly more active from 10:00 to 13:00 h (Figure 4): *O. cultriformis* ($\chi^2 = 74.96$, $df = 7$, $p < 0.0001$), *L. herculea* ($\chi^2 = 137.29$, $df = 7$, $p < 0.0001$), *O. discolor* ($\chi^2 = 69.06$, $df = 7$, $p < 0.001$), and *C. insularis* ($\chi^2 = 29.90$, $df = 7$, $p < 0.001$). *Erythrodiplax fervida* was equally active throughout the day ($\chi^2 = 8.68$, $df = 7$, $p > 0.05$, Figure 4).

The patterns of male diurnal activity (perch events h^{-1}) corresponded to radiation and temperature. Mean hourly solar radiation ($W m^{-2}$) increased from 08:00 to 11:00 h, plateaued between 11:00 and 13:00 h, and then dropped sharply (Figure 5). Mean hourly temperature rose from 08:00 h through the 14:00 h interval, and then declined more slowly than radiation (Figure 5). As expected, these variables were strongly (but not perfectly) correlated, as temperature change lagged behind changes in radiation (Pearson correlation, one-tailed, $r = 0.737$, $N = 8$, $p = 0.019$). For the four species with peak activity near mid-day (*C. insularis*, *O. cultriformis*, *O. discolor*, and *L. herculea*), mean hourly temperature and mean hourly solar radiation were significantly higher during the hourly intervals when individuals were present (observed perch event) than when they were absent (no observed perch event; Table 1). For these species, total perch events h^{-1} (corrected for differences in sampling effort per hourly interval) was more strongly related to radiation than temperature in multiple regression analyses (though not to a statistically significant degree for *L. herculea* or *O. cultriformis*; Table 2). For *Micrathyria atra*, which was most active in the morning, and *E. fervida*, which was active throughout the day, there were no significant differences in mean hourly temperature or mean hourly solar radiation between

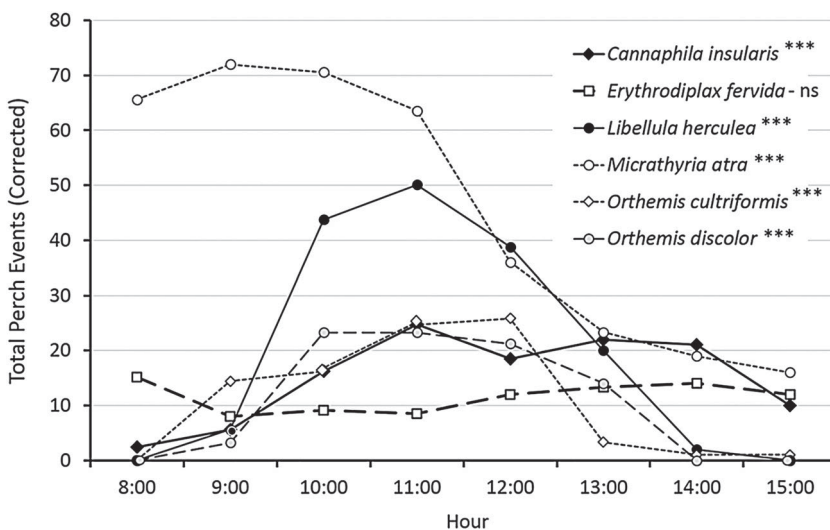


Figure 4. The frequencies of observed perch events per hour (corrected for differences in sampling effort) by males of the six most abundant species of libellulids in the Cantarrana Wetland, La Selva Biological Station, Heredia, Costa Rica. There were significant differences in hourly frequencies for all species but *E. fervida* (χ^2 goodness-of-fit tests, *** = $p < 0.001$, ns = $p > 0.05$).

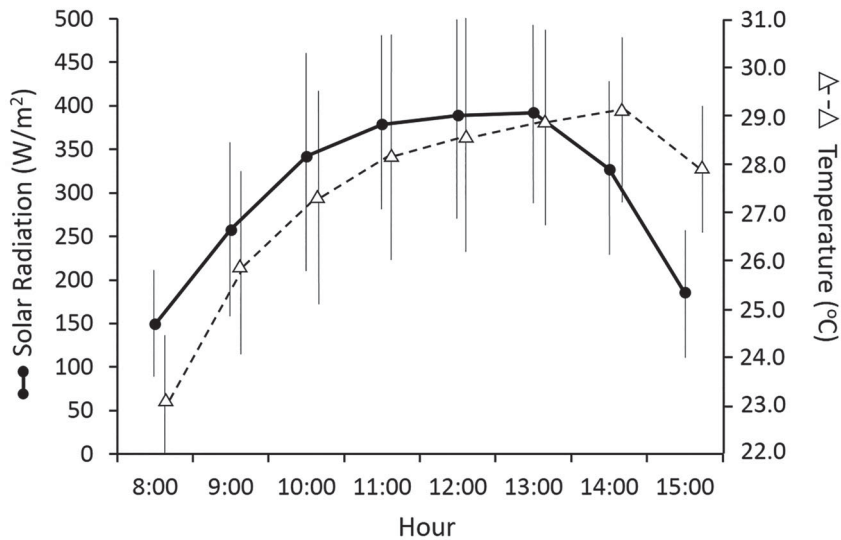


Figure 5. Mean (± 1 SD) solar radiation (W m^{-2} ; black line and black circles) and mean (± 1 SD) temperature ($^{\circ}\text{C}$; dashed line and white triangles) four hourly intervals sampled between 08:00 and 16:00, from 20 January to 8 February 2016, at La Selva Biological Station, Heredia, CR. Data computed from Organization for Tropical Studies (2016).

Table 1. Differences in (a) mean temperature ($^{\circ}\text{C}$) and (b) mean solar radiation (W m^{-2}) for sampled hourly intervals when common species were either present (at least one observed perch event) or absent (no observed perch event).

(a)		Present		Absent	
Species	N	$\bar{X} \pm 1$ SD	N	$\bar{X} \pm 1$ SD	t
<i>Cannaphila insularis</i>	75	28.11 \pm 2.11	48	25.86 \pm 3.05	4.48 ***
<i>Erythrodiplax fervida</i>	71	27.51 \pm 2.48	52	26.85 \pm 3.04	1.29 ns
<i>Libellula herculea</i>	42	28.89 \pm 1.41	81	26.37 \pm 2.86	6.55 ***
<i>Micrathyrta atra</i>	86	27.48 \pm 2.35	37	26.63 \pm 3.44	1.37 ns
<i>Orthemis cultriformis</i>	34	28.77 \pm 1.47	89	26.64 \pm 2.88	5.37 ***
<i>Orthemis discolor</i>	25	28.56 \pm 1.79	98	26.89 \pm 2.84	3.63 **
(b)		Present		Absent	
	N	$\bar{X} \pm 1$ SD	N	$\bar{X} \pm 1$ SD	t
<i>Cannaphila insularis</i>	75	350.96 \pm 133.49	48	238.10 \pm 129.53	4.66 ***
<i>Erythrodiplax fervida</i>	71	309.74 \pm 141.54	52	303.06 \pm 145.27	0.25 ns
<i>Libellula herculea</i>	42	389.96 \pm 101.97	81	263.86 \pm 142.03	5.66 ***
<i>Micrathyrta atra</i>	86	319.07 \pm 128.75	37	278.67 \pm 169.05	1.30 ns
<i>Orthemis cultriformis</i>	34	396.83 \pm 107.72	89	272.57 \pm 139.69	5.25 ***
<i>Orthemis discolor</i>	25	389.32 \pm 125.02	98	285.90 \pm 139.65	3.60 **

Note: Student's t-tests, ns = $p > 0.05$, ** = $p < 0.001$, *** = $p < 0.0001$.

periods when they were present or absent (Table 1). For *M. atra*, total perch events h^{-1} was negatively associated with increasing temperature, but activity of *E. fervida* was unrelated to either radiation or temperature (Table 2).

These patterns were also corroborated at a smaller scale: these six species used sunny, moderate, and shady perches at significantly different frequencies (χ^2 test of independence, $\chi^2 = 263.05$, $\text{df} = 10$, $p < 0.0001$, Figure 6). *Erythrodiplax fervida* preferred shaded perches ($\chi^2 = 26.72$, $\text{df} = 2$, $p < 0.0001$), *M. atra* preferred moderately sunlit perches ($\chi^2 = 61.60$, $\text{df} = 2$, $p < 0.0001$), and sunny perches were preferred by *L. herculea* ($\chi^2 = 81.77$, $\text{df} = 2$, $p < 0.0001$), *O. cultriformis* ($\chi^2 = 12.37$, $\text{df} = 2$, $p < 0.01$), and *O. discolor* ($\chi^2 = 111.16$,

Table 2. Summary of multiple regression analyses of the relationship between total perch events h^{-1} (corrected by differences in sampling effort) and mean hourly temperature and mean solar radiation (W m^{-2}) for periods sampled.

Species	R^2 model	F	p	Temperature		Radiation	
				t	p	t	p
<i>Cannaphila insularis</i>	0.913	26.160	0.002	1.312	0.25	3.843	0.01
<i>Erythrodiplax fervida</i>	0.214	0.681	0.548	0.572	0.59	-1.109	0.55
<i>Libellula herculea</i>	0.625	3.331	0.141	-0.971	0.39	2.333	0.08
<i>Micrathyrja atra</i>	0.710	6.115	0.045	-3.477	0.02	2.307	0.07
<i>Orthemis cultriformis</i>	0.411	1.744	0.266	-0.820	0.45	1.739	0.14
<i>Orthemis discolor</i>	0.695	5.703	0.051	-1.767	0.14	3.248	0.02

Note: Pearson correlation between temperature and solar radiation, one-tailed, $r = 0.737$, $N = 8$, $p = 0.019$.

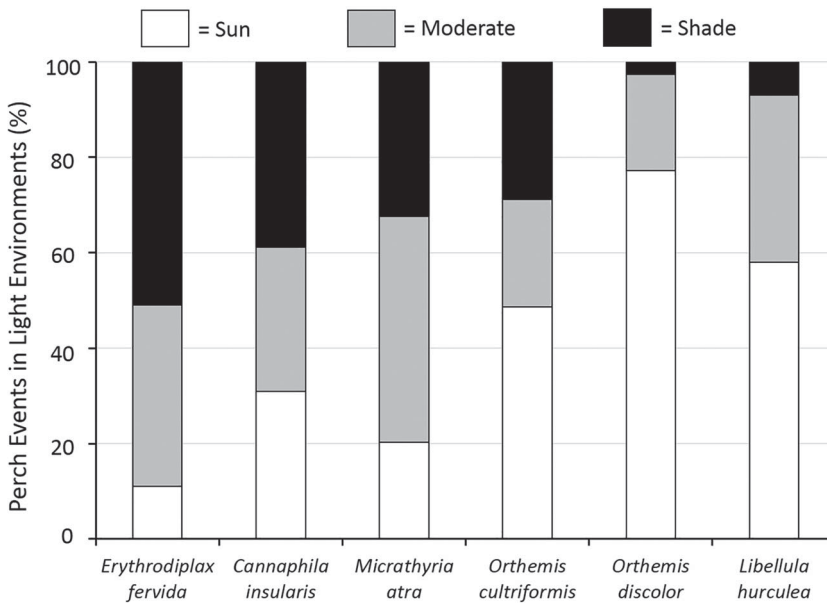


Figure 6. The proportion perches in sun, moderate sun, and shade by males of the six most abundant species of libellulids in the Cantarrana Wetland, La Selva Biological Station, Heredia, Costa Rica. Species are ordered by body size from small to large. Species differ in their light environment preferences (see results), and the percentage of perches in sun correlates with mean body size (two-tailed Pearson correlation, $r = 0.9256$, $p < 0.01$).

$df = 2$, $p < 0.0001$; Figure 6). *Cannaphila insularis* was the only common species that showed no preference ($\chi^2 = 2.06$, $df = 2$, $p > 0.05$; Figure 6). The percentage of perches in sun correlated with body size (Pearson correlation, two-tailed, $r = 0.9256$, $p < 0.01$).

There were statistically significant differences in the frequency of aggressive interactions by males of these six abundant species, when compared to expected frequencies based on their relative abundances ($\chi^2 = 251.99$, $df = 5$, $p < 0.0001$). *Cannaphila insularis* was particularly docile, with only one intraspecific attack and one attack on *L. herculea*. It was also rarely attacked, registering only two attacks from each of the four aggressive species, *L. herculea*, *M. atra*, *O. cultriformis*, and *O. discolor*. Likewise, *E. fervida* was rarely involved in interspecific encounters, registering only two attacks from *L. herculea* and never attacking another species. In contrast to *C. insularis*, however, *E. fervida* was a bit more pugnacious to conspecifics: there were 11 attacks between *E. fervida* males. Given the lack of interactions involving *C. insularis* and *E. fervida*, further analyses were limited to the four species frequently involved in

aggressive encounters. The two largest species, *L. herculea* and *O. discolor*, engaged in frequent interspecific interactions, attacking (and being attacked by) one another more frequently than their relative abundance would predict (Figures 7 and 8). In contrast, the two smaller species, *M. atra* and *O. cultriformis*, engaged primarily in intraspecific combat – attacking (and being attacked by) conspecifics more frequently than expected by their relative abundances (Figures 7 and 8).

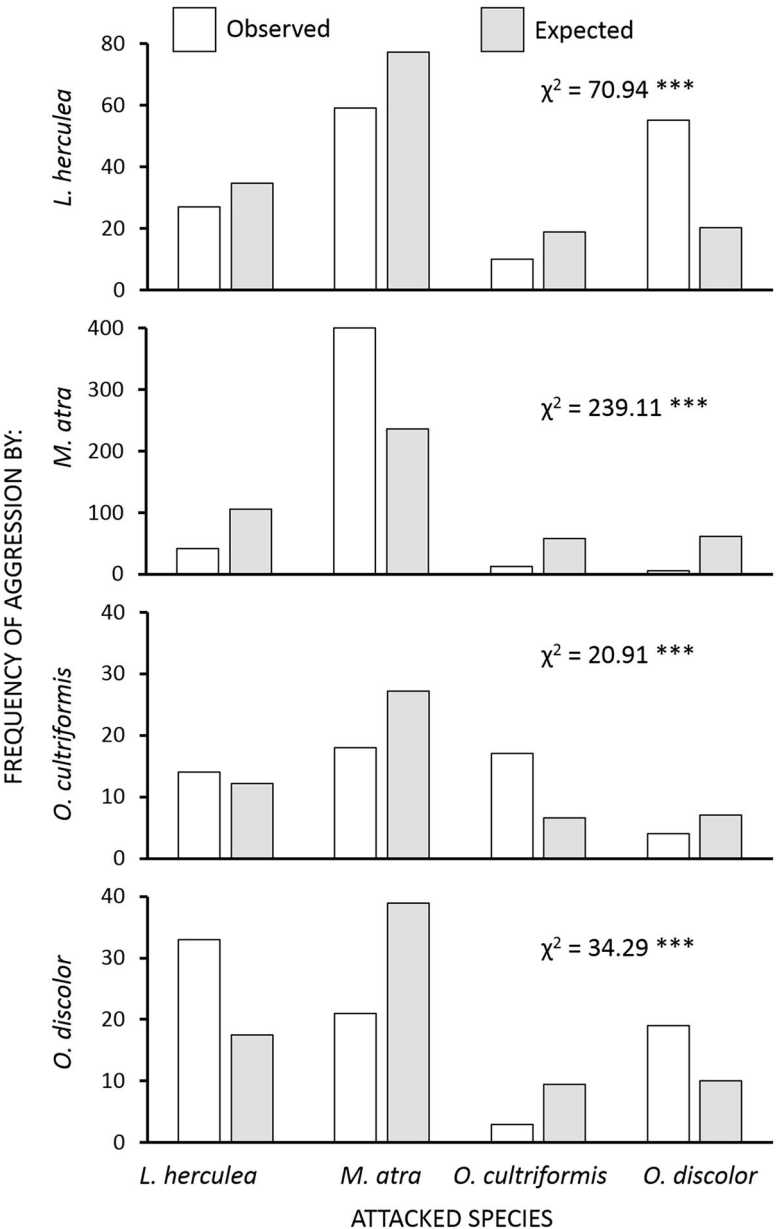


Figure 7. Patterns of aggression by males of four interacting libellulid species in the Cantarrana Wetland, La Selva Biological Station, Heredia, Costa Rica. Male of all species attacked other males at frequencies that were significantly different from expected by the relative abundances of these species (χ^2 goodness-of-fit tests, *** = $p < 0.001$).

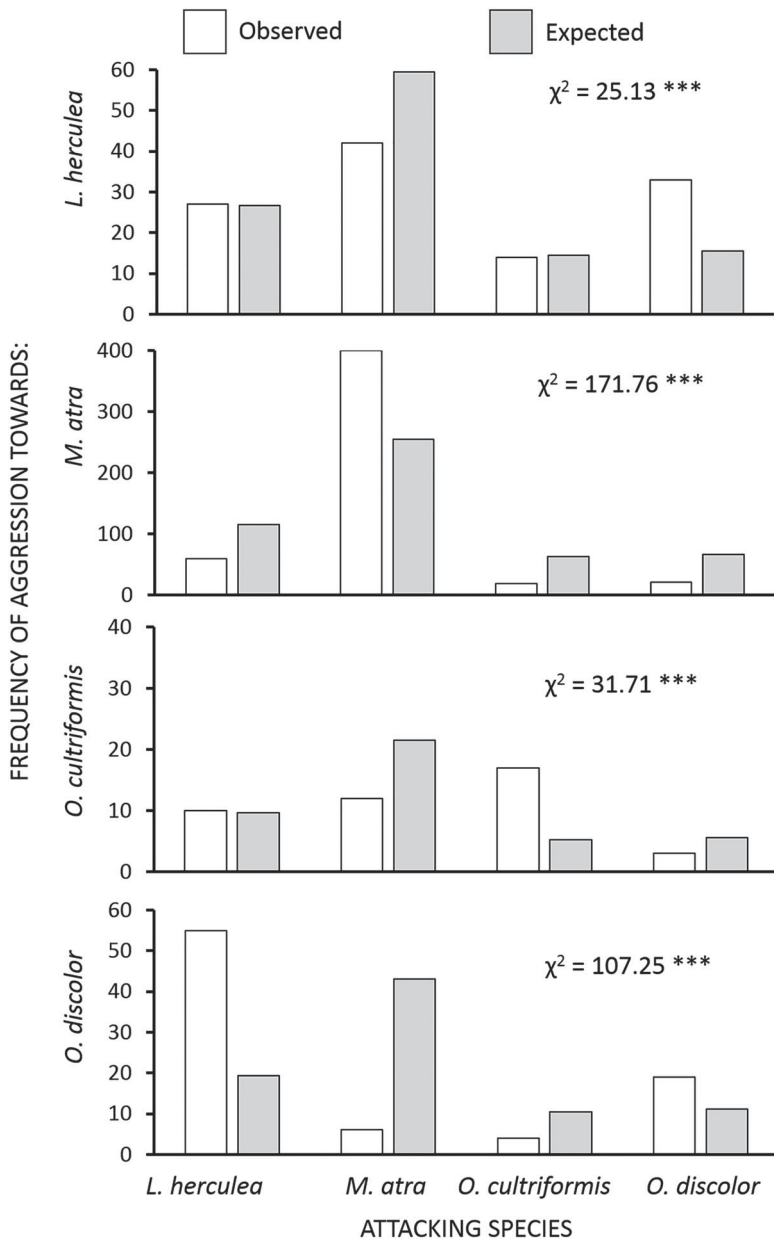


Figure 8. Patterns of aggression towards males of four interacting libellulid species in the Cantarrana Wetland, La Selva Biological Station, Heredia, Costa Rica. Males of all species were attacked by other males at frequencies that were significantly different from expected by the relative abundances of these species (χ^2 goodness-of-fit tests, *** = $p < 0.001$).

Discussion

Mean male perch height correlated with species' body size, confirming patterns found in temperate communities (Moore, 1991; Warren, 1964; Worthen & Jones, 2006). Although the community-level pattern was confirmed, one species departed dramatically from the relationship:

Cannaphila insularis is medium-sized but perched nearly a meter higher, on average, than any other species.

For most species, patterns of perch selection, diurnal activity, and intra- and interspecific aggression were consistent with predictions based on size (Warren, 1964; Worthen & Jones, 2006), thermal ecology (Corbet & May, 2008), niche overlap, and previous studies of these species (May, 1976, 1977; De Marco & Resende, 2004). *Erythrodiplax fervida*, the smallest species in the study, used low grasses almost exclusively – even though there were downed branches and the stems of small trees available in the same height range. Although the larger *E. umbrata* perched on downed twigs on occasion, all three *Erythrodiplax* species were extremely similar in their perching ecology. They were very secretive, perching for a long time and then rapidly darting to a neighboring perch – almost without a discernable intervening flight. They rarely interacted: *Erythemis fervida* was attacked 14 times, 11 times by conspecifics; and they never attacked another species. Esquivel (2006) reports that these are typical behaviors for juveniles, but that territorial males rarely perch and are often engaged in aggressive intraspecific interactions. There were many mature *E. fervida* in this study, however, so perhaps their behavior was suppressed by the presence of larger, more aggressive species. In addition, all three *Erythrodiplax* species perched in one grassy area, several meters away from open pools. This is also typical for small members of the genus: De Marco et al. (2005) found that *Erythrodiplax media* Borror, *Erythrodiplax paraguayensis* (Förster) and *Erythrodiplax ochracea* (Burmeister) – the smallest members of their community – perched more than other species and perched on bank vegetation rather than on emergent macrophytes in the pond. Curiously, *E. fervida* were equally active throughout the day, showing no response to changes in temperature or sunshine. Activity and abundance of small perchers is usually related to air temperature (May, 1976, 1991): congeners *Erythrodiplax fusca* (Rambur) and *E. media*, for example, are most active in mid-day during the dry season in Brazil (De Marco & Resende, 2002). Here, however, *E. fervida* may prefer shaded perches to reduce variation in temperature and radiation, or to hide from predators and larger, more aggressive competitors.

Micrathyria atra is a medium-sized libellulid that was active in the mornings and perched in shady or moderate sunlight at intermediate heights close to open pools, preferring grass blades but using downed branches and overhanging tree limbs near water. These are typical behaviors for *M. atra*, which uses behavioral adaptations to thermoregulate and avoid high temperatures and high radiational load (May, 1976, 1977). As predicted, they exhibited a weak positive relationship with radiation (to warm up to flight temperature), but a significant negative relationship with temperature over this temperature range. May (1977) observed that they fly continuously while air temperature is below 24°C, and suggested that they must either bask or wing-whir to reach flight temperature under these conditions. I confirmed May's (1977) hypothesis during this survey, observing an *M. atra* female wing-whir under shady conditions at 24.9°C (Worthen, 2016). Their high perching frequency and strong intraspecific aggression is typical of abundant species (De Marco et al., 2005).

The three largest common species, *O. cultriformis*, *O. discolor*, and *L. herculea*, exhibited the expected activity patterns for heliothermic perchers (Corbet & May, 2008; Heinrich & Casey, 1978). They preferred sunny perches and were most active at mid-day, as found for *O. discolor* in the dry season in Brazil (De Marco & Resende, 2002). Periods when they were present were significantly warmer and sunnier than absent periods, and radiation was a better predictor of activity than temperature in multiple regression. They usually perched in trees along the periphery of the pond, but there was some spatial partitioning: *L. herculea* frequently used downed branches close to central pools of open water, while the smaller *O. cultriformis* perched lower and used moderate and shady perches more frequently. Like the medium-sized *M. atra*, *O. cultriformis* may be more sensitive to heat stress than the larger species and may mediate these effects by using shady perches when it is active at mid-day.

Orthemis discolor and *L. herculea* occurred at much lower density than the other common species, with rarely more than one male of each species in the habitat at a time. This is typical for *O. discolor*, where single males may command an entire pond as a territory, and use high perches along the periphery to scan the entire habitat for females or intruding males (De Marco & Resende, 2004). Given their similar niche parameters, it is not surprising that *O. discolor* and *L. herculea* males were often engaged in aggressive interspecific contests.

Although the perch behavior of most species conformed to expectations based on size or thermoregulatory strategy, two species were intriguing exceptions. *Orthemis schmidtii* is a large species and should behave like its congeners – as a heliotherm. However, it was usually observed (five of seven observations) in the late afternoon on shady perches. The aberrant behavior of *Cannaphila insularis* – a well-sampled species – is more compelling. This medium-sized species perched nearly 1 m higher, on average, than any other libellulid in the community. Based on its size, it should be a thermoconformer. In most respects, however, it acted like a heliotherm: it was most active in the heat of the day, total perch events (activity) were better predicted by radiation than temperature, radiation levels were significantly higher when it was present than when it was absent, and it often perched in trees along the periphery of the habitat. Esquivel (2006) reports that males typically perch in the sun (reinforcing the heliotherm comparison), but Paulson (2009) reports that they typically perch in the shade. Indeed, it was the only species in this study to exhibit no preference for sunny or shady perches. In fact, they exhibited an extraordinary range of environmental tolerance, even flying and perching in the rain.

Cannaphila insularis may use extremely high perches to avoid interactions with larger, more aggressive species – particularly *O. cultriformis*. Of the common species, *O. cultriformis* is most similar to *C. insularis* in activity period, substrate selection, and perch-shading preferences – niche dimensions largely prescribed by thermoregulatory constraints that make encounters unavoidable – unless they partition perches vertically. In addition, immature males and females of *C. insularis* bear a strong resemblance to *O. cultriformis* females, and I observed a male *O. cultriformis* attempt to tandem with an immature male *C. insularis*. Perching high may be adaptive for *C. insularis* because it decreases aggression from *O. cultriformis*, and “reproductive interference” (Drury, Okamoto, Anderson, & Grether, 2015; Gröning & Hochkirch, 2008; Murray, 1981; Tynkkynen, Kotiaho, & Svensson, 2008) caused by “mistaken identity” (Shultz & Switzer, 2001). Santos and Machado (2016) suggest, in species like *C. insularis* where the females are more colorful and have more wing pigmentation than males, that female wing pigmentation may be adaptive as a “signal” of sexual maturity. Another possibility, consistent with the “reproductive interference” hypothesis, is that wing pigmentation is also an interspecific signal distinguishing *C. insularis* from *Orthemis* species – which are notably clear-winged in both sexes (Santos & Machado, 2016).

In conclusion, patterns of activity and perch selection in this community of tropical libellulids were largely consistent with predictions based on body size and thermal ecology. However, these patterns can change seasonally (De Marco & Resende, 2002), and the relationship between body size and perch height should be tested in the rainy season when more species are present. In addition, experiments could determine if perch height is a narrowly constrained adaptation or is behaviorally responsive to the presence of larger competitors. The unusual behavior of *O. schmidtii* – a presumed heliotherm perching in the shade – is anecdotal and needs confirmation. The consistent, exceptional perch-height behavior of *C. insularis* begs explanation. I hypothesize that their unusually high perch height is an adaptation to reduce interactions with larger, aggressive libellulids – interactions that may be a consequence of “mistaken identity” and the morphological similarity between juvenile and female *C. insularis* and *O. cultriformis* females.

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Supplemental data

Supplemental data for this article can be accessed at <http://dx.doi.org/10.1080/13887890.2017.1330225>.

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